

Variation in sense organ design and associated sensory capabilities among closely related molluscs

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Abstract. Knowledge of ontogenetic and interspecific variation in structural and functional properties of an organ is prerequisite to establishing valid generalizations about the organ's role within a group. However, for many molluscan sense organs, generalizations have become established with minimal knowledge of such variation. Review of data on the gross structure, optical properties and visual responses of 44 gastropods provides a clear example of this problem. Lens structures range from crystalline to gelatinous, with concomitant differences in refractive index, and degree of structural and optical homogeneity. Refractive index measurements from differential interference microscopy indicate that gastropod lenses could be partly or completely corrected for spherical aberration. Photoreceptor separation distances vary from about 3 to 25 μm , and photoreceptor abundances from about five to 100,000 per eye. Estimates of anatomical resolution vary from 0.25 to 14 degrees, and overlap considerably with values for arthropods and vertebrates. Visual responses range from simple taxis to the ability to detect an object's orientation. Reviews of data on the structure and function of opisthobranch rhinophores, and on scallop eye structure, also reveal greater variation than is typically appreciated. More attention must be given to variation in molluscan sense organ structure and function in order for this field to develop more fully.

The field of molluscan biology has been expanding its horizons over the past quarter century from its earlier emphasis on studies of taxonomy, shell morphology and anatomy (Solem, 1974), to greater exploration of life histories, ecological relationships, and behavior. Although few scientists with formal training in animal behavior specialized in studying molluscs 20 years ago, this is no longer true. Most animal behaviorists are still attracted to the more rapidly moving arthropods and vertebrates, but cephalopods have always presented a unique challenge, and the value of certain gastropods as neuroethological models has attracted numerous neurobiologists and some behaviorists, especially those interested in a reductionist approach. A computer search of literature citations dealing with the behavior of molluscs clearly demonstrates the rapid expansion of this subdiscipline (Fig. 1). More than 7,600 citations in Biological Abstracts have included information about molluscan behavior or sensory biology over the past 20 years, and the current rate of increase is about 500 citations per year.

The usual pattern of development in many biological subdisciplines is for initial studies to be conducted on one or two easily obtained species thought to be typical of a group, and for initial generalizations to be developed for the group based on the findings obtained for these 'type' species. Later, as is required for any field to mature, significant efforts must be directed toward consideration of a broad range of species. Information from comparative studies provides opportunities

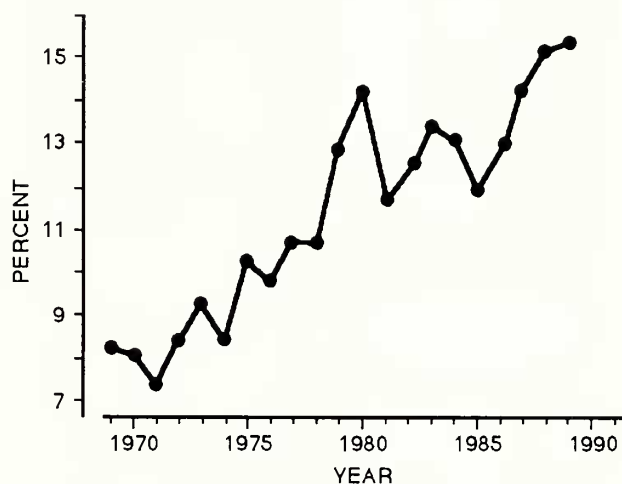


Fig. 1. Number of publications dealing with the behavior or sensory biology of molluscs, as a percentage of all publications dealing with molluscs, over the past two decades. These data are based on a computer search of Biological Abstracts, and should be considered only an approximation of the general trend.

to determine the phylogenetic limits of plasticity in the group, and often leads to revision of generalizations for the group and reconsideration of whether the initially studied species are indeed typical of the group.

Despite the substantial body of information already acquired on the behavior and sensory biology of molluscs, this

knowledge base is limited in several critical ways. Much of the information contained in the 7,600 citations noted above concerns just a handful of species, and the levels of intrageneric and intrafamilial variation have been hardly examined. In other cases intragroup variation has been examined and found to be considerable, but this does not seem widely appreciated. And finally, some of the 'type' species recognized by early investigators of molluscan behavior and sensory biology do not seem particularly representative in the context of the broader base of knowledge available today. Collectively, these factors would limit the validity of generalizations made about the behavior and sensory biology of any animal group. However, this is especially true for molluscs, as they have undergone an extensive adaptive radiation into a wide range of habitats, and they exhibit substantial plasticity in sense organ structure and behavior (Seed, 1983; Audesirk and Audesirk, 1985).

It seems, therefore, that substantially more attention needs to be given to the variation that exists within molluscan groups in the areas of behavior and sensory biology in order to resolve these problems and allow this field to achieve a more mature level of development. The goal here is to convince the reader of that viewpoint by examining three selected examples involving a range of taxonomic levels. First, eye structure and the behavioral function of vision in the entire Class Gastropoda will be reviewed in some detail. Then, briefer comparisons will be made of the structure and apparent behavioral function of a pair of head tentacles termed 'rhizophores' in the gastropod Subclass Opisthobranchia, and of the structure of the eyes in the bivalve Family Pectinidae (scallops).

GASTROPOD EYES AND VISUALLY MEDIATED BEHAVIOR

The primary example involves vision in gastropod molluscs. It has been traditional for zoologists (e.g. Messenger, 1981) to recognize three structural grades of eyes among the Gastropoda:

- a) the open cup or pit eye, in which the intraocular space is unfilled and not isolated from the surrounding medium by a cornea (e.g. *Patella*);
- b) the filled cup eye, in which a gelatinous (and hence low refractive index) material fills the intraocular space, but in which a cornea is lacking (e.g. *Haliotis*);
- c) the closed cup eye, in which a soft or hard lens is present in the intraocular space, and in which a cornea is present (e.g. *Nerita*, *Strombus*, *Littorina*).

Recognition of three grades of structure in gastropod eyes can describe, at best, but three points within what is a wide range of ocular designs. Furthermore, because two of the three traditionally recognized grades are exhibited only by quite primitive gastropods (e.g. *Patella*, *Haliotis*), this three

grade scheme cannot reflect adequately the range of variation present in gastropod eyes.

Land (1981, 1984) and Cronin (1988) have reviewed certain aspects of eye structure and optical properties in invertebrates, or particularly in molluscs, and limited efforts have been made to tabulate data on gastropod eyes (Zunke, 1978; Messenger, 1981; Land, 1984). Although many excellent studies have been made of retinal ultrastructure and neurophysiological responses, these studies have tended to provide incomplete or no information about whole eye structure or, importantly, the eye as a complete optical system. Thus, there are fewer published data than some might suspect on which to base any general conclusions about gastropod vision. A more detailed comparative view of eye structure in this group is provided here (Table 1) by pooling most of the published data, which covers about 32 species, with previously unpublished data on an additional 12 species.

Few authors who have studied gastropod eyes have reported retinal surface areas, or photoreceptor separation distances, abundances, and densities. Thus, most of the data in Table 1 are derived from my computations based on illustrations and data included in the references cited. Average intraocular diameter is the mean of the major axis (distance from pupil to retina along optic axis) and the minor axis (distance between opposite retinal surfaces along a line perpendicular to the major axis and mid-way along it). Retinal areas were computed based on an ellipsoidal model, using the major and minor axes described above, with subtraction of that portion of the ellipsoid's total surface area corresponding to the aperture, where no photoreceptors are located. In most cases, photoreceptor separation distances were obtained directly from an author's measurements or illustrations. However, for *Pterocera* (= *Lambis*) *lambis* (Linné) and *Aplysia californica* Cooper, the separation distances used here are 1 μm greater than the indicated photoreceptor diameters; this adjustment corresponds to a minimal thickness of supportive cells separating adjacent receptors. Receptor knowledge base is limited in several critical ways. Much of the information contained in the 7,600 citations noted above concerns just a handful of species, and the levels of intrageneric and intrafamilial variation have hardly been examined. In other cases intragroup variation has been examined sides whose length equals the receptor separation distance). A hexagonal model matches the actual spatial positions of photoreceptors seen in ideal sections taken tangential to the inner retinal surface, for a variety of gastropods (e.g. Hamilton *et al.*, 1983). Receptor densities were computed from retinal area and receptor abundance values. For lens sizes, a single value is given for spherical lenses, and the order of the two values listed for oblong lenses represents the lengths parallel and perpendicular to the optic axis, respectively. Shell length was used as a measure of body length, except in species where the shell is clearly reduced or absent. The length

Table 1. Variation in eye structure among selected gastropod molluscs.

Taxon	Adult Length (mm)	Mean Intraoc. Diam. (μm)	Retinal Area (mm ²)	Receptor Separ. Dist. (μm)	Receptor Abund.	Receptor Density (mm ⁻²)	Lens Diam. (μm)	Reference/Source
PROSOBRANCHIA								
<i>Haliotis discus</i> Reeve	150	840	1.703	10.0	19665	11550	n/a	Tonosaki (1967)
<i>Turbo castanea</i> Gmelin	16	514	0.555	2.7	89840	161980	385 +	a
<i>Neritina reclivata</i> (Say)	15	248	0.161	5.7	5735	35540	235 +	a
<i>Littoraria irrorata</i> (Say)	19	233	0.109	4.4	6565	60470	170	Hamilton <i>et al.</i> (1983)
<i>Littorina littorea</i> (Linné)	22	143	0.052	12.0	415	8030	110	Newell (1965)
<i>Tectarius muricatus</i> (Linné)	19	178	0.074	4.5	4210	57030	141	a
<i>Strombus luhuanus</i> Linné	40	1184	3.025	6.0	97020	32080	732	Gillary (1974), Gillary and Gillary (1979)
<i>Pterocera lambis</i> (Linné)	90	1023	2.893	12.0	23200	8020	1023	Prince (1955)
<i>Lioplax pilsbryi</i> Walker	28	220	0.121	5.5	4610	38210	165x150	a
<i>Pomacea paludosa</i> (Say)	50	561	0.775	4.0	55940	72170	440x322	a
<i>Elimia curvicostata</i> (Reeve)	15	103	0.028	4.5	1600	57030	112x104	a
<i>Marginella</i> sp.	9	120	0.031	6.5	835	27330	102	a
<i>Nassarius vibex</i> (Say)	13	197	0.085	6.9	2050	24250	150x165	a
<i>Melongena corona</i> (Gmelin)	76	273	0.166	7.9	3075	18510	215x175	a
OPISTHOBRANCHIA								
<i>Bulla gouldiana</i> Pilsbry	50	327	0.285	12.5	2110	7390	300x225	Jacklet and Colquhoun (1983)
<i>Aplysia brasiliiana</i> Rang	178	507	0.613	16.0	2765	4510	388x297	a
<i>A. californica</i> Cooper	216	471	0.572	16.0	2585	4520	450x400	Jacklet and Geronimo (1971), Herman and Strumwasser (1984)
<i>Hermisenda crassicornis</i> (Eschscholtz)	—	—	—	—	5	—	35x50	Stensaas <i>et al.</i> (1969)
<i>Tritonia diomedea</i> (Bergh)	—	—	—	—	5	—	150x130	Chase (1974)
Mean for 16 nudibranchs	—	—	—	—	8	—	57	Hughes (1970)
PULMONATA								
<i>Melampus bidentatus</i> Say	13	101	0.018	7.4	375	21210	63x100	a
<i>Lymnaea stagnalis</i> (Linné)	28	140	0.050	10.0	585	11610	110x100	Stoll (1973)
<i>Biomphalaria glabrata</i> (Say)	17	212	0.121	14.8	640	5290	163x131	Schall and Baptista (1990)
<i>Strophocheilus</i> sp.	120	350	0.338	23.8	690	2040	291x240	Oswaldo-Cruz and Bernardes (1982)
<i>Euglandina rosea</i> (Férussac)	63	177	0.083	5.0	3825	46210	175x150	a
<i>Helix aspersa</i> Müller	36	231	0.134	6.3	3890	29120	225x200	Eakin and Brandenburger (1975), Brandenburger (1975)
<i>Succinea putris</i> (Linné)	17	97	0.026	14.7	145	5490	60x70	Zunke (1978)
<i>Limax flavus</i> Linné	88	209	0.132	15.0	680	5160	145x175	Kataoka (1975, 1977)
<i>Agriolimax reticulatus</i> Müller	43	94	0.013	20.0	40	3150	87x67	Newell and Newell (1968)

+ = Additional lens protrusion through aperture. a = Based on author's previously unpublished observations.

values used were those stated in the references indicated in Table 1 or, when authors failed to indicate the sizes of the animals studied, those given as average adult sizes in appropriate basic references.

Starting at the largest scale, one can consider the relative sizes of the eyes in adults of various species. Figure 2 shows the relationship between the mean diameter of the intraocular space and the body length of adults for 26 species distributed among three subclasses. Two points are clear from this analysis. First, the size of the intraocular space varies fairly widely among gastropods, with *Strombus luhuanus* Linné having an average intraocular diameter more than 12 times greater than *Agriolimax reticulatus* Müller. Second, average intraocular diameter is significantly correlated with

body length when all three subclasses are pooled together ($r=0.43$, $P=0.030$), and for the subclasses Prosobranchia ($n=14$, $r=0.62$, $P=0.019$) and Pulmonata ($n=9$, $r=0.75$, $P=0.019$) when analyzed separately. Opisthobranchs were not analyzed separately because reasonable measures of intraocular diameter are available for only three species. Gastropod eyes can be positioned within a substantial perioptic sinus, as in littorinids (Newell, 1965; Hamilton *et al.*, 1983), or they can be closely surrounded by connective tissue, as in *Aplysia californica* (Herman and Strumwasser, 1984).

As would be expected, lens size (as measured by area in mid-sagittal section) is highly correlated with average intraocular diameter ($r=0.87$, $P<0.0001$) and the amount of

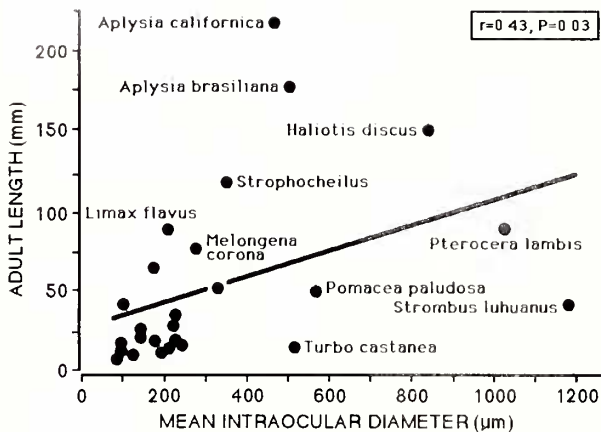


Fig. 2. Relationship between the mean diameter of the intraocular space and the adult body length of 26 gastropods from three subclasses. The species associated with the outlying points are identified. Significant positive correlations also exist for just the prosobranchs ($n=14$) and just the pulmonates ($n=9$).

retinal surface area ($r=0.97$, $P<0.0001$). The abalone *Haliotis discus* Reeve lacks a lens, as reportedly do *Trochus* and *Patella* (Hilger, 1885), but the eyes of all other gastropods surveyed here have a lens or lens-like material located in the intraocular space. Optical properties of lenses are influenced partly by their shape. Lens shapes vary from spherical or nearly so, as in the littorinids, strombids and *Lymnaea*, to ellipsoidal, as in various prosobranchs, the aplysiids and most pulmonates (Table 1). Some amount of vitreous material is present between the lens and retina in most species, although Dorsett (1986) suggests this is not the case. Past confusion concerning the presence or absence of vitreous material in the eyes of various species could have been due to the susceptibility of vitreous material to dissolution during histological processing (Charles, 1966; Hamilton *et al.*, 1983).

The lens of *Aplysia californica* was originally illustrated as being spherical, and filling the entire intraocular space (Jacklet *et al.*, 1972). This report led logically to the conclusion that its eye could not form a sharp image (Messenger, 1981; Dorsett, 1986) because of insufficient distance for light rays to be brought to focus on the retina (Land, 1981). However, the illustration in Jacklet *et al.* (1972) is based apparently on an earlier section of the eye in which no aperture was visible, indicating that the section was oblique rather than longitudinal (Jacklet, 1969). A more recent study by Herman and Strumwasser (1984) has shown clearly that the *A. californica* lens and intraocular space are quite ellipsoidal, as is the case in *A. brasiliana* Rang. This finding will hopefully stimulate reconsideration of the visual capabilities of this species.

In addition to these general shape patterns, the lenses of some gastropods exhibit unique shape variants. The opisthobranch *Navanax* (= *Aglaia*) *inermis* (Cooper) possesses a distinctly bilobed lens, the function of which is

unknown (Eskin and Harcombe, 1977). In the eye of *Turbo castanea* Gmelin, a portion of the lens protrudes through the aperture, and this protrusion of the lens has a shorter radius of curvature than the main body of the lens located within the intraocular space. Because the focal length of a curved refractive surface is directly proportional to its radius of curvature, the protruding portion of lens causes the entire *T. castanea* lens to have a shorter focal length than it would otherwise have, making focus of light on the retina more likely. A wider field of view should also result from this 'fish-eye' lens, but this is probably less significant for *T. castanea*. Similar lens protrusions were described for *Turbo creniferus* Kiem. and *Nerita polita* Linné (Hilger, 1885), and *Neritina reclinata* (Say) also possesses a distinct lens protrusion.

Gastropod lenses vary considerably in hardness. The literature contains numerous pictures of shattered lenses, and it appears that hard lenses are more common than soft lenses in gastropods. However, exact description of lens hardness is difficult, and besides apparent lens hardness (as indicated by degree of shattering when sectioned) seems to be influenced somewhat by the fixative and embedding medium used when processing eyes for histological examination (Hamilton *et al.*, 1983). Hardness is generally correlated with refractive index, a physical property directly relevant to vision. Authors have frequently noted a concentric pattern of stain uptake by gastropod lenses (e.g. Newell, 1965; Jacklet and Colquhoun, 1983; Gibson, 1984), and have inferred from this that such lenses vary concentrically in composition, and presumably refractive index. Gibson (1984) reported that polyhedral subunits, apparently composed of protein, were packed more densely towards the lens center in *Ilyanassa obsoleta* (Say).

Refractive index patterns or gradients within lenses or other structures can be measured exactly from frozen sections using differential interference microscopy. Land has successfully employed this technique with various invertebrates (e.g. Land and Burton, 1979), although data for the lenses of gastropods have not previously been published. In this technique, the distance that an interference fringe is displaced at any given point depends upon the refractive index at that point, as well as light wavelength and specimen thickness, both of which can be controlled.

Preliminary data for the marsh periwinkle, *Littoraria irrorata* (Say), reveal a distinct refractive index gradient within its spherical lens, which is only 170 μm in diameter (Fig. 3). [Reid (1986) moved this species from the genus *Littorina*.] This gradient closely matches the theoretical gradient required for complete correction of spherical aberration (the curve in Fig. 3; based on Fletcher *et al.*, 1954), a major source of potential image degradation. Preliminary data obtained for the ellipsoidal *Aplysia brasiliana* lens also indicate a refractive index gradient, ranging from about 1.40 at the periphery to about 1.51 at the core. The *Turbo castanea* lens varies in

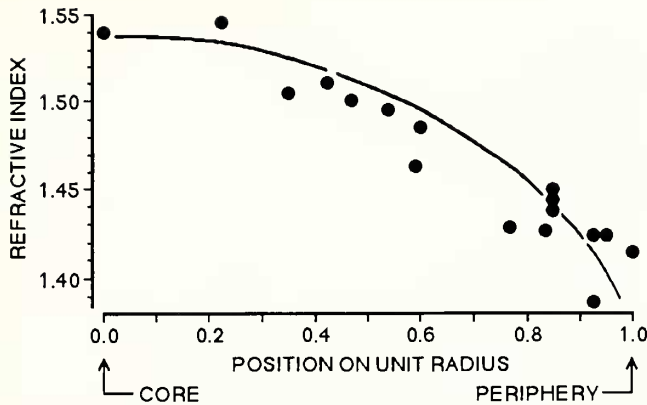


Fig. 3. Refractive index values at different points in the 170 μm diameter spherical lens ($f/r=2.71$) of the marsh periwinkle, *Littoraria irrorata*, as measured using differential interference microscopy. The curve indicates the refractive index gradient required for perfect correction of spherical aberration in a spherical lens ($f/r=2.70$) surrounded by a medium whose refractive index is 1.365, which is the average value of cornea and vitreous material.

refractive index from 1.40 at the cornea to 1.45 near the lens center, so even soft lenses can have refractive index gradients. The optical significance of a refractive index gradient is unclear for species with relatively soft lenses, and lenses with non-spherical surfaces. Substantial spherical aberration could exist in such eyes, or spherical aberration could be eliminated if corneal surfaces are parabolic, instead of spherical. In addition to reducing spherical aberration, refractive index gradients also produce a shorter-than-expected focal length, a result which could be as or more important in some species.

Gastropod eyes also vary substantially in retinal and photoreceptor properties (Table 1). Nudibranchs must be considered separately because they clearly exhibit extreme reduction of the eye. For example, Hughes (1970) found that 16 species of nudibranchs had an average of only eight (8) photoreceptors per eye. A survey of the 26 non-nudibranch species on which data are available reveals that retinal areas vary from 0.013 mm^2 (*Agriolimax reticulatus*) to 3.025 mm^2 (*Strombus luhuanus*), a factor of about 230 times. Most gastropods' photoreceptors contain few or no melanin pigment granules, and so contrast strongly with supportive cells. The photoreceptor counts or estimates reported in the literature have been obtained by various methods. My data on photoreceptor size and spacing have been obtained from sections tangential to the inner retinal surface. As shown in Table 1, adjacent photoreceptors are separated by distances varying from 2.7 μm (*Turbo castanea*) to 23.8 μm (*Strophocheilus* sp.) Photoreceptor abundances per eye vary from 40 (*Agriolimax reticulatus*) to 97,020 (*Strombus luhuanus*), a factor of about 2,500 times. These photoreceptor abundance values should be viewed only as estimates because at least some gastropods possess two or more receptor types, and these may not be easily distinguished at the light microscope level. Also, photoreceptor densities are known

to differ in different regions of the retina in *Littoraria irrorata* (Hamilton *et al.*, 1983) and *Aplysia californica* (Herman and Strumwasser, 1984).

Variation in lens or retinal properties can even be substantial within a family or genus. The greatest variation encountered thus far appears to be among the littorinids. When compared with *Littorina littorea* (Linné), *Littoraria irrorata* has twice the retinal area and a three times shorter receptor separation distance, which results in almost 16 times more receptors per eye (Table 1). *L. irrorata* is active in air, while *L. littorea* appears principally active when submerged in water. That difference in behavioral ecology is probably associated with the substantial difference in eye structure, because the degree to which light is refracted at the cornea depends greatly upon the refractive index of the surrounding medium. *Tectarius muricatus* (Linné), another littorinid, is active in air. Although it has a retinal area intermediate between the other two littorinids, it has a receptor separation distance and total receptor abundance that are much more similar to the littorinid active in air, *L. irrorata*. These similarities in retinal design are related presumably to the higher light levels present in air. Unfortunately, the data available for the eye of *Littorina scutulata* Gould (Mayes and Hermans, 1973) do not allow evaluating the eye as an optical system.

Variation in eye structure in littorinids can be explained by differences in behavioral ecology, but the situation is less clear in other cases of variation between closely related gastropods. Within the Strombidae, *Strombus luhuanus* and *Pterocera* (= *Lambis*) *lambis* have similarly sized eyes, but *S. luhuanus* has twice as closely spaced receptors and hence four times more receptors than *P. lambis*. The receptor which Prince (1955) illustrated for *P. lambis* is 6 μm in diameter; however, he indicated that the average receptor diameter is 11 μm , and his estimate of total receptor density ("something approaching" 10,000/ mm^2) generally agrees with the estimate in Table 1, which is based on a receptor separation distance of 12 μm . Both strombid species are active in shallow water. *S. luhuanus* is about half the size and travels almost nine times more slowly than *Pterocera* (= *Lambis*) *lambis* (Berg, 1974), yet the *S. luhuanus* eye seems capable of resolving greater detail. Berg (1974), who studied ten strombids, noted specifically that *S. luhuanus* seemed "to be able to sense the position" of a predatory cone snail, but he did not speculate on the sensory modality involved. No obvious differences are apparent in eye structure between the two *Aplysia* species listed, beyond the disagreement mentioned earlier about shape of intraocular space and lens. This is somewhat surprising because the species seem to exhibit basic behavioral differences. *A. brasiliiana* is an excellent swimmer and is active principally at night. In contrast, *A. californica* apparently does not swim at all, and is diurnally active in the lab and field; whether it may also be nocturnally active under

natural conditions remains unknown (Hamilton, 1986; Leonard and Lukowiak, 1986).

Vision in various species can most accurately be compared, not by any of the numbers in Table 1, but rather by knowing the resolving power of the eye. Several factors can influence resolution, but one useful estimate of resolution is the angular separation of adjacent receptors relative to the 'optical center' of the eye (the posterior or proximal nodal point). Resolution measures or estimates have been published for *Littorina littorea* (Newell, 1965), *Littoraria irrorata* (Hamilton *et al.*, 1983), *Strombus luhuanus* (Land, 1984), *Haliotis discus* (Land, 1981), *Biomphalaria glabrata* (Say) (Schall and Baptista, 1989), and *Strophocheilus* sp. (Oswaldo-Cruz and Bernardes, 1982), and reasonable estimates can be computed for a few other gastropods. These resolution values are given in figure 4, along with comparative data for selected arthropods and vertebrates from Kirschfeld (1976). Clearly the resolving powers possessed by gastropod eyes exhibit a wide range, and they overlap considerably with the resolving powers of arthropod and vertebrate eyes.

As Audesirk and Audesirk (1985) suggests, the assumption that vision plays only a minor role in gastropod behavior has had an inhibitory influence on careful studies of visually-mediated behavior in this group. It is commonly believed that the structurally-simple eyes of gastropods only mediate simple phototaxis or skototaxis, orientation toward or away from light or dark areas, respectively. However, critical experiments have rarely been done that could allow discrimination between true phototaxis or skototaxis, and form vision, however crude or simple. Hopefully, the existing collection of anecdotes and

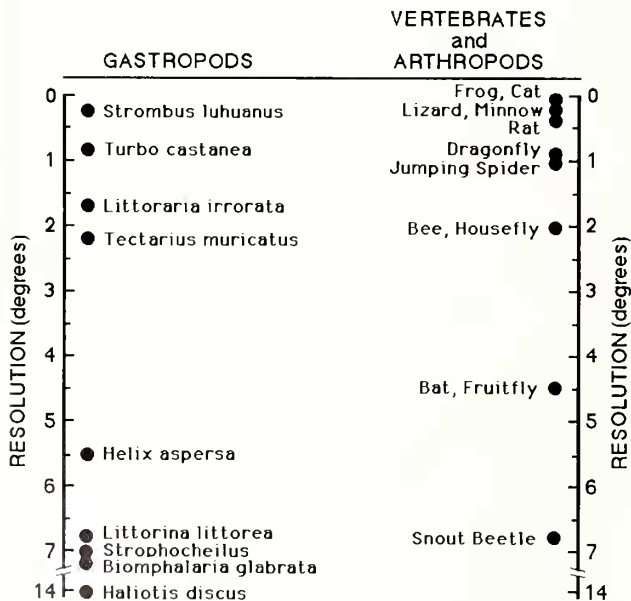


Fig. 4. Measures and estimates of anatomical resolution for nine species of gastropod, with comparative data for selected vertebrates and arthropods.

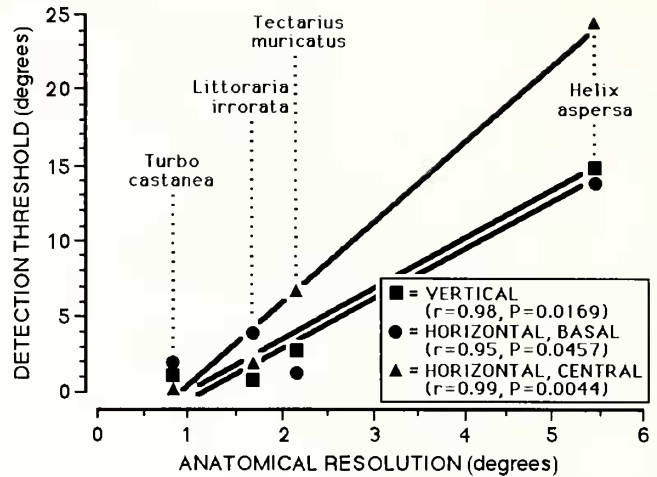


Fig. 5. Measures and estimates of anatomical resolution, and behavioral 'detection' thresholds for oriented responses to three types of targets (vertical stripe, centrally-positioned horizontal stripe, basally-positioned horizontal stripe), for four species of gastropod.

weakly founded assertions about gastropod vision will eventually be replaced with carefully obtained data delineating their visual capabilities.

Standardized behavioral measures of visual detection have been obtained for four of the gastropod species discussed here (Hamilton and Winter, 1982, 1984), and these compare well with the previously mentioned anatomical resolution measures and estimates (Fig. 5). Also, it is clear that at least *Littoraria irrorata* can distinguish details of an object's orientation; it preferentially moves toward a vertical black stripe on a white background when presented with horizontal or diagonal stripes having equivalent width and contrast (Hamilton and Winter, 1982). Because the *L. irrorata* eye is not qualitatively different from that of many other gastropods, it could well be that other species can distinguish such visual detail too. Both *Tectarius muricatus* and *Turbo castanea* show some ability to discriminate target orientation (Hamilton and Winter, 1984). An unblocked view of the sky is required for *Aplysia brasiliana* to maintain its swimming direction, which suggests sensitivity to complex visual cues (Hamilton and Russell, 1982a).

In summary, the assortment of optical tricks encountered in the eyes of various vertebrates, including fish eye lenses and lenses with refractive index gradients, are also found among gastropods. This high degree of variation in gastropod eyes should not be viewed as counter-intuitive. The fishes, for example, are less diverse in habitat and general morphology than the gastropods, yet their eyes exhibit an extensive range of adaptations correlated with habitat and behavioral strategy (Lythgoe, 1980; Fernald, 1988). As Land (1981) has noted, there is no clear break within the range of resolving powers exhibited by the eyes of animals. There really is no such thing as an image forming eye as distinct from

a non-image forming eye. There are only degrees of need for visual detail among animals, and degrees of image quality provided by eyes. For gastropods and other invertebrates, assumptions about vision, based on vertebrocentric biases, need to be replaced by more hard data and a genuine comparative perspective.

OPISTHOBRANCH RHINOPHORES

This is one of the most obvious cases of unappreciated variation in molluscan sensory biology, and a classic example of why biologists should avoid assigning names to structures that are based on assumed functions. The rhinophores are a pair of tentacles located near the eyes on the dorsal surface of the head, and hence in the same location as the pair of tentacles termed the 'cephalic tentacles' in prosobranch gastropods. The name 'rhinophore' literally means bearer of the nose or nasal sense. This name appears to have been coined by Bergh (1879), who worked principally with the predatory nudibranchs, a group in which the rhinophores do seem involved in distance chemoreception in many species. MacFarland's (1966) treatise on opisthobranchs beautifully illustrates the structural diversity of nudibranch rhinophores. In many species, rhinophoral sheaths are present, as well as numerous lamellae projecting laterally from a central axis. The greatly increased surface area provided by the lamellae is itself suggestive that nudibranch rhinophores have a chemosensory function in this carnivorous group.

However, if one takes a more comparative approach, and looks at other opisthobranch taxa, it is clear that other feeding strategies exist, and that the so-called rhinophores can have a variety of different structural features and sensory functions. In the herbivorous *Aplysia*, for example, each rhinophore has a simple gross structure, with no basal sheath and no lamellae. A pigmented groove on the distal half of the rhinophore receives most of the innervation (Fig. 6; from Ronan, 1990). Despite this much simpler gross structure, aplysiid rhinophores have been implicated in chemoreception, mechanoreception (touch, waves, currents) and even photoreception (Frings and Frings, 1965; Jahan-Parwar, 1972; Audesirk, 1975; Chase, 1979; Jacklet, 1980; Hamilton and Russell, 1982b). It could be that variation exists in rhinophore sensory function, even among *Aplysia* species, since substantial variation exists in morphology, activity rhythms and swimming behavior among aplysiids (Eales, 1960; Hamilton, 1986).

Inadequate appreciation for the variation in rhinophore morphology, feeding strategy and key behavioral traits between nudibranchs and other opisthobranchs has led to the incorrect assumption that the sensory functions associated with the rhinophores of a predatory group (the nudibranchs) automatically apply to other opisthobranch groups. A general under-appreciation for diversity within opisthobranchs could

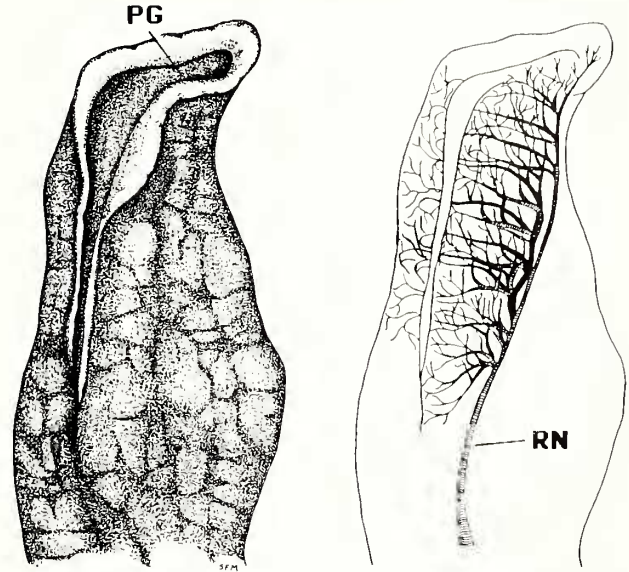


Fig. 6. External view showing the pigmented groove (PG) of the *Aplysia brasiliana* rhinophore (left), and internal view showing the rhinophoral nerve (RN) and its innervation pattern (right), based on analysis of serial sections (from Ronan, 1990, with permission). A fully extended rhinophore is 15-20 mm long in adults.

be partly responsible for this problem, but the literal meaning of 'rhinophore' is probably the primary factor. Beginning ethologists are taught the importance of selecting names for the discrete behaviors included in an ethogram based on spatial and temporal features of the movement pattern involved, rather than on the presumed adaptive function of the behavior. For example, the cyclic lateral movement of the siphon which appears when various neogastropods become alerted to a prey's proximity would be named something like 'siphon waving' rather than 'odor searching'. Anatomists are presumably taught some similar rule, and certainly the 'issue' of opisthobranch rhinophores would be less confused today if such a standard had been followed in the 1800's. The confusion that the term rhinophore has caused over the years suggests that we could be better off just referring to these opisthobranch structures as cephalic tentacles, as we do for the seemingly homologous paired tentacles of prosobranch gastropods. Admittedly, the term 'tentacle' suggests a tactile sensory function, but mechanoreception seems a general property of virtually all such structures, regardless of what additional sensory capability they can exhibit.

SCALLOP EYES

Scallops (family Pectinidae) are swimming bivalve molluscs which possess about 60-100 eyes distributed along the mantle edges. The detailed studies of Land (1965) on *Pecten maximus* (Linneé) revealed the presence of a unique double-layered retina in each eye, and an equally unique

optical system dependent upon a reflector at the rear of the eye, whose surface is described as spherical. Importantly, Land's analyses show little or no space between the rear of the lens and the retina, or between the retina and the reflective argentea. This is in contrast to Dakin's (1928) earlier study of *Pecten maximus*, which reported a space between the lens and retina about 20% of the eye's length. Butcher (1930) found no space between the lens and retina of *Pecten* (= *Argopecten*) *gibbus* (Linné) but he found a space occupying about 40% of the eye's length between the retina and argentea of this species. In a preliminary study of the eye of *Argopecten irradians* (Lamarck), Wooters (1989) found a space having a similar size and location to that reported by Butcher, and an argentea which appeared more parabolic than spherical. Finally, considerable variation exists in the sizes of the eyes possessed by individuals in at least some scallop species. This variation could be due to differences in developmental or regenerative growth, but this appears unstudied with the exception of Butcher's (1930) work on *Pecten* (= *Argopecten*) *gibbus*. Perhaps the apparent interspecific differences in scallop eye structure are due to different investigators describing eyes at different growth stages in different species.

As with gastropod molluscs, any genuine interspecific differences in scallop eye structure could also be associated with differences in behavior or ecology. *Argopecten irradians* are found in water less than 4 m deep, particularly in beds of the seagrass *Thalassia*, whose blades reach as high as 0.4 m above the bottom. In contrast, *A. gibbus* and *Pecten maximus* are both found in water deeper than 10 m, typically on substrata consisting of sand and shell fragments. Hence, these three scallops differ in the amount of biologically relevant visual detail in their environments, as well as in water depth and associated light characteristics. How these habitat differences or behavioral traits could be associated with differences in eye structure is unknown. Wooters (1969) found that *A. irradians* orient visually toward grassbeds when released in sand patches adjacent to grassbeds, but little is known of the behavioral role of vision in other scallops.

In summary, detailed comparative studies need to be completed to determine exactly what ontogenetic and interspecific variation exists in scallop eye structure and optical properties. Although the eyes of the various scallop species seem generally similar, the available information on eye structure suggests that some interspecific differences could exist in optical properties, especially as regards focal point position and the degree of spherical aberration. Insufficient attention to interspecific variation can easily lead to confusion, and possibly even errors in interpretation. For example, McReynolds and Gorman (1970) studied the electrophysiological properties of the eye of *Pecten* (= *Argopecten*) *irradians*, but included a "Pecten eye" diagram based on Dakin's (1928) illustration of the eye of *Pecten maximus*. It

seems prudent to exercise caution in extrapolating structural, physiological and behavioral results across scallop species until detailed comparative studies are conducted.

CONCLUSION

This review of gastropod vision, opisthobranch rhinophores and scallop eyes demonstrates that there exists considerable variation in sensory system design and capabilities among molluscs, even within families or genera. In the case of gastropod eyes, considerable progress has been made in documenting substantial variation, and the problem seems that the observed variation is underappreciated. In the case of scallop eyes, interspecific variation has barely been documented, yet preliminary results encourage detailed comparative study in the future. The case of opisthobranch rhinophores seems somewhat intermediate; appreciation that the function implied by the name rhinophore might not apply to many opisthobranchs has existed at least since Arey (1918), yet little progress has been made toward obtaining a satisfactory comparative view of the behavioral and ecological correlates of the variations in structure found in this group.

Additional evidence of substantial interspecific variation will likely be obtained eventually for other sense organs, such as the statocyst and osphradium. Statocyst structure has been examined for a modest number of molluscs (Budelmann, 1988), but the possible behavioral-ecological correlates of observed structural diversity have hardly been explored. The literature contains some interesting and apparently paradoxical cases which beg for analysis. For example, the benthic gastropod *Pomacea paludosa* (Say) possesses about 3,000 sensory cells in its statocyst, while a mere 13 cells are present in the statocyst of *Aplysia limacina* de Blainville (= *A. fasciata* Poiret), which is one of the many aplysiids which has been reported to swim as well as crawl on the bottom (Dijkgraaf and Hessels, 1969; Stahlschmidt and Wolff, 1972). Analysis of osphradial variation and its basis across molluscs is complicated by the fact that the name osphradium has sometimes been assigned to structures that are clearly not homologous.

The presence of this substantial interspecific variation emphasizes the necessity of communicating about particular organisms and sense organs more carefully and, where possible, more exactly. The limits and bases of variation would be more easily understood if more authors would include specific information about the sizes of the actual animals they studied, as well as the relationship between sense organ dimensions and body size in the species. Zünke's (1978) study of the eye of *Succinea* includes detailed coverage of ontogenetic variation and, unfortunately, it is unusual in doing so. Failure to consider intraspecific or ontogenetic variation can lead to generalizations just as premature and flawed as those based on too few or atypical species. Autrum (1979) pointed out that it is clearly a bad habit to speak just of "the

fly" in scientific writings. Likewise, it can be a bad habit to speak just of "the littorinid", "the rhinophore" or "the scallop", depending on what species, system or capability is being discussed.

Finally, as more comparative data become available, it should become possible to discard some of the less informative terms in general use for sensory structures. For example, there have existed in the invertebrate literature several terms for structurally simple eyes. 'Pigment cup eyes' and 'pinhole eyes', which both lack lenses, have widely accepted definitions based on structural features (see Land, 1981). However, 'eyespot' and 'ocellus' both mean "a very small simple eye formed in invertebrates." As has so often been the case in invertebrate zoology, the emphasis seems to have been on establishing the existence of a difference as compared to the vertebrate eye, rather than on recognizing the various invertebrate eyes as being distinct structures worthy of independent study and understanding.

As a relatively new field, many gaps exist in our knowledge of molluscan behavior and sensory biology. A clearer understanding would be provided about sensory capabilities within groups if more species were examined, and this would also allow more thorough investigation of the basis of existing variation across species. However, more effort should also be devoted to completing the data sets for species about which some information is already available. In many cases, only data on structure of sense organs or sensory tissues are available from which to draw inferences about function; obviously the availability of data from electrophysiological and behavioral studies would be desirable in such instances. For example, scallop eye structure and electrophysiological responses have received some study, but there is little understanding of how well they can see or what adaptive value vision has in nature. A reasonably complete range of data are available for only a few cases, mostly involving species that serve as model systems for neurobiologists. Thus, future researchers in molluscan sensory biology should be encouraged to flesh out existing stories, as well as to expand our understanding of variability within the group by examining as-yet-unstudied species.

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LITERATURE CITED

- Arey, L. B. 1918. The multiple sensory activities of the so-called rhinophores of nudibranchs. *American Journal of Physiology* 46:526-532.
- Audesirk, T. E. 1975. Chemoreception in *Aplysia californica*. 1. Behavioral localization of distance chemoreceptors used in food finding. *Behavioral Biology* 15:45-55.
- Audesirk, T. and G. Audesirk. 1985. Behavior of gastropod molluscs. In: *The Mollusca*, Volume 8, A. O. D. Willows, ed., pp. 1-94. Academic Press, New York.
- Autrum, H. 1979. Preface. In: *Handbook of Sensory Biology*, Volume VII/6A, H. Autrum, ed. pp. v-vii. Springer-Verlag, Berlin.
- Berg, J. C. 1974. A comparative ethological study of strombid gastropods. *Behaviour* 51:274-322.
- Bergh, R. 1879. On the nudibranchiate gastropod Mollusca of the north Pacific Ocean, with special reference to those of Alaska. *Proceedings of the Academy of Natural Sciences* 1879:71-132, 1880:40-127.
- Brandenburger, J. L. 1975. Two new kinds of retinal cells in the eye of a snail, *Helix aspersa*. *Journal of Ultrastructure Research* 50:216-230.
- Budelmann, B-U. 1988. Morphological diversity of equilibrium receptor systems in aquatic invertebrates. In: *Sensory Biology of Aquatic Animals*, J. Atema, R. R. Fay, A. N. Popper and W. N. Tavolga, eds. pp. 757-782. Springer-Verlag, New York.
- Butcher, E. O. 1930. The formation, regeneration, and transplantation of eyes in *Pecten (gibbus borealis)*. *Biological Bulletin* 59:154-164.
- Charles, G. H. 1966. Sense organs (less cephalopods). In: *Physiology of Mollusca*, Volume II, K. M. Wilbur and C. M. Yonge, eds. pp. 455-521. Academic Press, New York.
- Chase, R. 1974. The electrophysiology of photoreceptors in the nudibranch mollusc, *Tritonia diomedea*. *Journal of Experimental Biology* 60:707-719.
- Chase, R. 1979. Photic sensitivity of the rhinophore in *Aplysia*. *Canadian Journal of Zoology* 57:698-701.
- Cronin, T. W. 1988. Vision in marine invertebrates. In: *Sensory Biology of Aquatic Animals*, J. Atema, R. R. Fay, A. N. Popper and W. N. Tavolga, eds. pp. 403-418. Springer-Verlag, New York.
- Dakin, W. J. 1928. The eyes of *Pecten*, *Spondylus*, *Amussium* and allied lamellibranchs, with a short discussion on their evolution. *Proceedings of the Royal Society of London, B* 103:355-365.
- Dijkgraaf, S. and H. G. A. Hessels. 1969. Über bau und funktion der statocyste bei der schnecke *Aplysia limacina*. *Zeitschrift für vergleichende Physiologie* 62:38-60.
- Dorsett, D. A. 1986. Brains to cells: the neuroanatomy of selected gastropod species. In: *The Mollusca*, Volume 9, A. O. D. Willows, ed. pp. 101-187. Academic Press, New York.
- Eakin, R. M. and J. L. Brandenburger. 1975. Understanding a snail's eye at a snail's pace. *American Zoologist* 15:851-863.
- Eales, N. B. 1960. Revision of the world species of *Aplysia* (Gastropoda: Opisthobranchia). *Bulletin of the British Museum of Natural History, Zoology* 5:268-404.
- Eskin, A. and E. Harcombe. 1977. Eye of *Navanax*: optic activity, circadian rhythm and morphology. *Comparative Biochemistry and Physiology* 57A:443-449.
- Fernald, R. D. 1988. Aquatic adaptations in fish eyes. In: *Sensory Biology of Aquatic Animals*, J. Atema, R. R. Fay, A. N. Popper and W. N. Tavolga, eds. pp. 435-466. Springer-Verlag, New York.
- Fletcher, A., T. Murphy and A. Young. 1954. Solutions to two optical problems. *Proceedings of the Royal Society of London, A* 223:216-225.
- Frings, H. and C. Frings. 1965. Chemosensory bases of food-finding and feeding in *Aplysia juliana* (Mollusca: Opisthobranchia). *Biological Bulletin* 128:211-217.
- Gibson, B. L. 1984. Cellular and ultrastructural features of the adult and the embryonic eye in the marine gastropod, *Ilyanassa obsoleta*. *Journal of Morphology* 181:205-220.
- Gillary, H. L. 1974. Light-evoked electrical potentials from the eye and optic nerve of *Strombus*: Response waveform and spectral sensitivity. *Journal of Experimental Biology* 60:383-396.

- Gillary, H. L. and E. W. Gillary. 1979. Ultrastructural features of the retina and optic nerve of *Strombus luhuanus*, a marine gastropod. *Journal of Morphology* 159:89-116.
- Hamilton, P. V. and M. A. Winter. 1982. Behavioural responses to visual stimuli by the snail, *Littorina irrorata*. *Animal Behavior* 30:752-760.
- Hamilton, P. V. and B. J. Russell. 1982a. Celestial orientation by surface-swimming *Aplysia brasiliana* Rang (Mollusca: Gastropoda). *Journal of Experimental Marine Biology and Ecology* 56:145-152.
- Hamilton, P. V. and B. J. Russell. 1982b. Field experiments on the sense organs and directional cues involved in offshore-oriented swimming by *Aplysia brasiliana* Rang (Mollusca: Gastropoda). *Journal of Experimental Marine Biology and Ecology* 56:123-143.
- Hamilton, P. V., S. C. Ardizzoni and J. S. Penn. 1983. Eye structure and optics in the intertidal snail, *Littorina irrorata*. *Journal of Comparative Physiology* 152:435-445.
- Hamilton, P. V. and M. A. Winter. 1984. Behavioural responses to visual stimuli by the snails *Tectarius muricatus*, *Turbo castanea*, and *Helix aspersa*. *Animal Behavior* 32:51-57.
- Hamilton, P. V. 1986. Swimming tracks of *Aplysia brasiliana*, with discussion of the roles of swimming in sea hares. *Veliger* 28:310-313.
- Herman, K. G. and F. Strumwasser. 1984. Regional specializations in the eye of *Aplysia*, a neuronal circadian oscillator. *Journal of Comparative Neurology* 230:593-613.
- Hilger, C. 1885. Beitrage zur Kenntnis des Gastropodenauges. *Morphologisches Jahrbuch* 10:351-371.
- Hughes, H. P. I. 1970. A light and electron microscope study of some opisthobranch eyes. *Zeitschrift für Zellforschung und mikroskopische Anatomie* 106:79-98.
- Jacklet, J. W. 1969. Electrophysiological organization of the eye of *Aplysia*. *Journal of General Physiology* 53:21-42.
- Jacklet, J. W. and J. Geronimo. 1971. Circadian rhythm: population of interacting neurons. *Science* 174:299-302.
- Jacklet, J. W., R. Alvarez and B. Bernstein. 1972. Ultrastructure of the eye of *Aplysia*. *Journal of Ultrastructure Research* 38:246-261.
- Jacklet, J. W. 1980. Light sensitivity of the rhinophores and eyes of *Aplysia*. *Journal of Comparative Physiology* 136:257-262.
- Jacklet, J. W. and W. Colquhoun. 1983. Ultrastructure of photoreceptors and circadian pacemaker neurons in the eye of a gastropod, *Bulla*. *Journal of Neurocytology* 12:673-696.
- Jahan-Parwar, B. 1972. Behavioral and electrophysiological studies on chemoreception in *Aplysia*. *American Zoologist* 12:525-537.
- Kataoka, S. 1975. Fine structure of the retina of a slug, *Limax flavus* L. *Vision Research* 15:681-686.
- Kataoka, S. 1977. Ultrastructure of the cornea and accessory retina in a slug, *Limax flavus* L. *Journal of Ultrastructure Research* 60:296-305.
- Kirschfeld, K. 1976. The resolution of lens and compound eyes. In: *Neural Principles in Vision*, F. Zettler and R. Weiler, eds. pp. 354-372. Springer-Verlag, Berlin.
- Land, M. F. 1965. Image formation by a concave reflector in the eye of the scallop, *Pecten maximus*. *Journal of Physiology* 179:138-153.
- Land, M. F. and F. A. Burton. 1979. The refractive index gradient in the crystalline cones of the eyes of a euphausiid crustacean. *Journal of Experimental Biology* 82:395-398.
- Land, M. F. 1981. Optics and vision in invertebrates. In: *Handbook of Sensory Physiology*, Volume VII/6B, H. Autrum, ed. pp. 471-594. Springer-Verlag, Berlin.
- Land, M. F. 1984. Molluscs. In: *Photoreception and Vision in Invertebrates*, M. A. Ali, ed. pp. 699-725. Plenum Press, New York.
- Leonard, J. L. and K. Lukowiak. 1986. The behavior of *Aplysia californica* Cooper (Gastropoda: Opisthobranchia): I. Ethogram. *Behaviour* 98:320-360.
- Lythgoe, J. N. 1980. *The Ecology of Vision*. Clarendon Press, Oxford. 244 pp.
- MacFarland, F. M. 1966. Studies of Opisthobranchiate Mollusks of the Pacific Coast of North America. *Memoirs of the California Academy of Science*, Vol. VI. 546 pp..
- Mayes, M. and C. O. Hermans. 1973. Fine structure of the eye of the prosobranch mollusk *Littorina scutulata*. *Veliger* 16:166-168.
- McReynolds, J. S. and A. L. F. Gorman. 1970. Photoreceptor potentials of the opposite polarity in the eye of the scallop, *Pecten irradians*. *Journal of General Physiology* 56:376-391.
- Messenger, J. B. 1981. Comparative physiology of vision in molluscs. In: *Handbook of Sensory Physiology*, Volume VII/6C, H. Autrum, ed. pp. 93-200. Springer-Verlag, Berlin.
- Newell, G. E. 1965. The eye of *Littorina littorea*. *Proceedings of the Zoological Society of London* 144:75-86.
- Newell, P. F. and G. E. Newell. 1968. The eye of the slug *Agriolimax reticulatus* (Mull.). *Symposium of the Zoological Society of London* 23:97-111.
- Oswaldo-Cruz, E. and R. F. Bernardes. 1982. Morphological and functional observations on the eye of *Strophocheilus* (Mollusca, Gastropoda, Stylommatophora). *Brazilian Journal of Medical and Biological Research* 15:161-174.
- Prince, J. H. 1955. The molluscan eyestalk: using as an example, *Pterocera lambis*. *Texas Reports on Biology and Medicine* 13:323-339.
- Reid, D. G. 1986. The littorinid molluscs of mangrove forests in the Indo-Pacific region: the genus *Littoraria*. *British Museum (Natural History), London*. 227 pp.
- Ronan, M. P. 1990. A review of opisthobranch rhinophores with a study of *Aplysia* rhinophore structure. Master's Thesis, University of West Florida, Pensacola, Florida. 113 pp.
- Schall, V. T. and D. F. Baptista. 1989. Structural and functional analysis of the eye of *Eiomphalaria glabrata* (Mollusca, Gastropoda, Basommatophora). *Brazilian Journal of Medical and Biological Research* 22:497-508.
- Seed, R. 1983. Structural organization, adaptive radiation, and classification of molluscs. In: *The Mollusca*, Volume 1, P. W. Hochachka, ed. pp. 1-54. Academic Press, New York.
- Solem, G. A. 1974. *The Shell Makers*. John Wiley, New York. 289 pp.
- Stahlschmidt, V. and H. G. Wolff. 1972. The fine structure of the statocyst of the prosobranch mollusc *Pomacea paludosa*. *Zeitschrift für Zellforschung und mikroskopische Anatomie* 133:529-537.
- Stensaas, L. J., S. S. Stensaas and O. Trujillo-Cenóz. 1969. Some morphological aspects of the visual system of *Hermisenda crassicornis* (Mollusca: Nudibranchia). *Journal of Ultrastructure Research* 27:510-532.
- Stoll, C. J. 1973. Observations on the ultrastructure of the eye of the basommatophoran snail, *Lymnaea stagnalis* (L.). *Proceedings of Koninklijke Nederlandse Akademie van Wetenschappen, Ser. C*, 76(4):1-11.
- Tonosaki, A. 1967. Fine structure of the retina in *Haliotis discus*. *Zeitschrift für Zellforschung und mikroskopische Anatomie* 79:469-480.
- Wooters, J. S. 1989. The ecology of vision in the bay scallop, *Argopecten irradians* (Pectinidae: Bivalvia). Master's Thesis, University of West Florida, Pensacola, Florida. 57 pp.
- Zunke, U. 1978. Bau und Entwicklung des auges von *Succinea putris* (Linné, 1758) (Mollusca, Stylommatophora). *Zoologischer Anzeiger* 3:220-244.